Bulletin

OF THE CHICAGO ACADEMY OF SCIENCES



Understanding Chimpanzees: Diversity and Survival

December 11-15, 1991 Chicago, Illinois

Symposium Abstracts

Bulletin

OF THE CHICAGO ACADEMY OF SCIENCES

Understanding Chimpanzees: Diversity and Survival

December 11-15, 1991 Chicago, Illinois

Symposium Abstracts

The *Bulletin* of The Chicago Academy of Sciences was instituted in 1883, and Volumes 1-4 were established prior to June 1913. During the following 20 years, the Bulletin was not issued. Volumes 1, 2, and 4 contain technical or semi-technical papers on various subjects in the natural sciences. Volume 3 contains museum reports, descriptions of museum exhibits, and announcements.

Publication of the *Bulletin* was resumed in 1934 with Volume 5. The series is now regarded as an outlet for submitted papers, short to moderate in length, on natural history. The *Bulletin* is edited by the Academy staff, with the assistance of outside reviewers. The separate numbers, issued at irregular intervals, are distributed to libraries and scientific organizations with whom the Academy maintains exchanges. A reserve is set aside for future exchanges, and the remainder of the edition is offered for sale at a nominal price.

Paul G. Heltne, President

Direct manuscript submissions and reprint orders to:

The Chicago Academy of Sciences 2001 North Clark Street Chicago, IL 60614

Attn: Bulletin

Phone 312-549-0606

A list of publications is available for \$3.00

Design: Michael Thibodeau, Chicago Cover illustration: Kevin McHugh, Chicago

© 1992 The Chicago Academy of Sciences

TABLE OF CONTENTS

OVERVIEWS

The Importance of Understanding Diversity Jane Goodall	
Explaining Diversity: Ecology and History in the Lives of Chimpanzees <i>Richard W. Wrangham</i>	
Chimpanzee Natural History and Its Importance for Understanding the Human Career Randall L. Susman	
The African Apes: A Review of Behavioral Diversity (Public Session) <i>Diane Doran</i>	
Behavioral Diversity: The Problem of Comparative Ethography (Workshop Summary) Jan A. R. A. M. van Hooff	3
SOCIO-ECOLOGY	
ECOLOGICAL AND ANATOMICAL PERSPECTIVES ON BEHAVIOR	
The Locomotor Behavior of Chimpanzees and Pygmy Chimpanzees Diane Doran	4
Sex Differences in Chimpanzee Positional Behavior, Activity Budget, and Diet Kevin D. Hunt	4
Ecological Determinants of Behavior: Comparisons between Lomako and Kibale Frances J. White and Colin Chapman	5
	5

FEEDING ECOLOGY

Comparative Feeding Ecology of Bonobos, Gorillas, and Chimpanzees Suehisa Kuroda	
Implications of Site Differences in Food Selection by Chimpanzees G. Isabirye-Basuta and Richard W. Wrangham	
The Relative Importance of Terrestrial Herbs for Bonobos and Chimpanzees: Comparative Data from Lomako and Kibale Richard Malenky and Richard W. Wrangham	7
Eating a Dead Colobus Monkey (Video Presentation) Christopher Boehm	7
Hunting Scenes of Mahale M Group Chimpanzees (Video Presentation) Hiroyuki Takasaki	8
Food-Related Behavior in Bonobos (Video Presentation) Amy <i>Parish</i>	8
TOOL USING	
Tools Compared: The Material of Culture? W. C. McGrew	8
Nut-Cracking Behavior and Environment at Bossou Tetsuro Matsuzawa and Yukimaru Sugiyama	9
At the Roots of Objectivity: Termite Fishing in Chimpanzees (Video Presentation) I. Eibl-Eibesfeldt	9
Tool-Using Scenes of Mahale M Group Chimpanzees (Video Presentation) Hiroyuki Takasaki	9
Bonobo Tool-Using Behavior (Video Presentation) Suehisa Kuroda	10
Two Methods of Dipping for Army Ants (Video Presentation) Christopher Boehm	10

SOCIAL RELATIONSHIPS

FIGHTING AND RECONCILIATION

Food-Sharing, Reciprocity, and Moralistic Aggression in Chimpanzees Frans B. M. de Waal	11
Competition, Cooperation, and Tension Regulation in a Community:	
Ethological Studies at the Arnhem Chimpanzee Consortium	11
Jan A. R. A. M. van Hooff	
Conflict Interactions among Male Chimpanzees at Mahale (Film and Discussion)	12
Shigeo Uehara	
Triadic Interventions (Video and Discussion)	12
Christopher Boehm	
Reconciliation Patterns among Newly Introduced Captive Chimpanzees	
(Video and Discussion)	13
Kate Baker, Susan McDonald Black, and Barbara Smuts	
Fighting and Reconciliation (Video Presentation)	13
Toshisada Nishida	
Fighting and Reconciliation (Video Presentation)	14
Frans B. M. de Waal	
Fighting and Reconciliation in Bonobos (Video Presentation)	14
Takayoshi Kano	
MOTHER-INFANT BEHAVIOR	
Weaning Conflict in Chimpanzees	14
Toshisada Nishida	
Mother-Infant Behavior	15
Jane Goodall	
The Adoption of Two Orphaned Chimpanzees at the Detroit Zoo (Video Presentation)	15
Susan McDonald Black and Kate Baker	
Mother-Infant Scenes of Mahale M Group Chimpanzees (Video Presentation)	16

SOCIAL RELATIONSHIPS

Effect of a Mother's Death on Her Offspring's Social Relationships with Group Members: Bonobos at Wamba, Zaire Takayoshi Kano	16
VOCALIZATION	
Dialects in Wild Chimpanzees?	17
John C. Mitani, Toshikazu Hasegawa, Julie Gros-Louis, Peter Marler, and Richar	d Byrne
Rank Differences in Vocal Production of Kibale and Gombe Chimpanzees as a Function of Social Context Adam P. Clark	17
SEXUAL BEHAVIOR	
Development and Change in the Social Role of Bonobo Sexual Behavior Takeshi Furuichi and Chie Hashimoto	18
Copulatory Behavior of <i>Pan paniscus</i> , Lomako Forest Nancy Thompson-Handler	19
Nonreproductive Sexual Behavior in Bonobos (Video Presentation) Amy Parish	19
PLAY	
Play Scenes of Mahale M Group Chimpanzees (Video Presentation) Hiroyuki Takasaki	20
Play Behavior (Video Presentation) Christopher Boehm	20
Play among Unfamiliar Adult Chimpanzees at the Detroit Zoo (Video Presentation) Kate Baker and Susan McDonald Black	20
The Play-Initiation Gestures of Young Chimpanzees (Video Presentation)	21

GROUP SPECIFIC BEHAVIOR

Group Specific Behavior: Mahale (Video Presentation) Toshisada Nishida	21
Intergroup Encounter of Bonobos in a Natural Forest (Video Presentation) Takeshi Furuichi	22
Group Specific Behavior (Video Presentation) Frans B. M. de Waal	22
Behavioral Diversity in Solitary Play at Arnhem (Video Presentation) Jan A. R. A. M. van Hooff	22
COGNITION	
Language from <i>Pan</i> to Man Sue Savage-Rumbaugh	23
Contributions from Studies of Cognition to Chimpanzee Conservation: Numerical and Inferential Processes Sarah T. Boysen	23
Why Do Chimpanzees Attribute Mental States to Others? Daniel Povinelli and Lucian Hughes	24
Ai: The Chimpanzee Mind (Public Session) Tetsuro Matsuzawa	24
Perception and Cognition from the Perspective of Comparative Cognitive Science Tetsuro Matsuzawa	25
Private Signing and Imagination Roger S. Fouts, Deborah H. Fouts, Mary Lee Abshire, and Mark Bodamer	25
Tool Use among Bonobos in the Wild and the Social Dimensions of Intelligence Ellen J. Ingmanson	26
Comparing the Ontogeny of Symbol Use in Pan paniscus and Homo sapiens Patricia M. Greenfield and Sue Savage-Rumbaugh	26

Comparison of Imitative Learning by Chimpanzees, Educated Chimpanzees,	
and Human Children (Video Presentation)	27
Michael Tomasello	
Cognition, Consciousness, and Their Adaptive Significance (Discussion Introduction) Jan A. R. A. M. van Hooff	27
CONSERVATION ISSUES IN AFRICA	
OVERVIEWS	
Problems of Chimpanzee Conservation and Care in Africa Jane Goodall	28
Chimpanzee Conservation: Actions and Options Geza Teleki	28
Impact on West African Chimpanzee Populations of Poaching for the Live Trade Margery L. Oldfield	29
International Trade in Chimpanzees: Problems and Solutions Michael A. O'Connell and Kurt A. Johnson	29
Conservation Issues in Africa (Slide Presentation) Chimpanzees: Do They Have a Future in Africa? (Slide Presentation, Public Session) Michael "Nick" Nichols	30
COUNTRY REPORTS	
Uganda Update Richard W. Wrangham	30
Status of Chimpanzees in Gabon Caroline E. G. Tutin and Michel Fernandez	31
Census and Distribution of Chimpanzees in Côte d'Ivoire Paul Marchesi, Nathalie Marchesi, and Christophe Boesch	31
Bonobo Conservation in the Wild Suehisa Kuroda	32
An Experiment in Long-Term Conservation Annette Lanjouw	32

SANCTUARIES

Chimfunshi Wildlife Orphanage Carole Noon	33
RESEARCH AND CONSERVATION IN CAPTIVITY	
RESEARCH	
Environmental Enrichment in Captivity Mollie Bloomsmith	34
ChimpanZoo: Looking at Chimpanzee Behavior in Contemporary Zoos Virginia Landau, James E. King, and Maryanne Clark	34
ChimpanZoo (Video Presentation) Virginia Landau, James E. King, and Maryanne Clark	35
Using Novel Objects to Facilitate Exploration and Play, and Reduce Aberrant Behaviors in the Chimpanzee Group at Adelaide Zoo (Poster Presentation) Carla Litchfield	35
CONSERVATION	
An Overview of the Chimpanzee Species Survival Plan Les Schobert	30
The Bonobo Species Survival Plan: Beyond Captive Management Gay E. Reinartz	30
Bonobo Conservation Task Force Update Bill Konstant	31
Captive Care and Management in Japan Tetsuro Matsuzawa	37

RELATED CONTRIBUTIONS (POSTERS AND WORKSHOPS)

RESEARCH SITE OVERVIEWS

Mahale Update (Poster Presentation) Toshisada Nishida	38
Wamba Update (Poster Presentation) Takayoshi Kano	38
Kibale Update (Poster Presentation) G. Isabirye-Basuta, Colin Chapman, Kevin D. Hunt, and Richard W. Wrangham	39
Pan paniscus in the Lokofe-Lilungu Region, Zaire (Poster Presentation) Jordi Sabater Pi and Joaquim J. Veá	39
Chimpanzees <i>(Pan troglodytes troglodytes)</i> of the Ndoki-Nouabale Forest, Northern Congo (Poster Presentation) Suehisa Kuroda and Rufin A. Oko	40
Nest Building in Wild Bonobos (Pan paniscus) in the Lomako Forest (Poster Presentation) Barbara Fruth and Gottfried Hohmann	40
Ishasha River Project (Poster Presentation) Jeanne Sept, Horst D. Steklis, and Mubalama Kakira	41
GENETICS	
Non-Invasive Sampling of DNA from Wild Chimpanzees (Workshop Presentation) Hiroyuki Takasaki and Osamu Takenaka	42
Application of New Genetic Techniques (Workshop Summary) Maryellen Ruvolo and Hiroyuki Takasaki	42
Strategies for the Genetic Management of Captive Chimpanzee Colonies (Poster Presentation) S. Williams-Blangero and B. Dyke	43
INTERACTIVE MEDIA	
The Jane Goodall Research Center at the University of Southern California: Using an Interactive Multimedia System (Demonstration) Gary Seaman and Homer Williams	43

PREFACE

The Chicago Academy of Sciences is pleased to present this special publication resulting from the international symposium "Understanding Chimpanzees: Diversity and Survival." In addition to abstracts of research papers, we include summaries of the numerous video presentations and the posters.

The symposium, organized and hosted by the Academy in December 1991, brought together prominent chimpanzee specialists from around the world – Africa, Europe, Asia, and North America –to examine the behavioral diversity and survival of chimpanzees and bonobos, both in the wild and in captivity. The contributors took a comparative approach to a wide range of topics, including social behavior and ecology, the rich variety of cultural traditions between populations, and the significant cognitive abilities of chimpanzees and bonobos. Presenters addressing the survival and well-being of these species examined population status in the wild, threats to habitat and survival, development of sanctuaries, and conservation and care in captivity. The abstracts include observations from field sites across Africa and from zoos and captive colonies.

In the planning stages of the conference, we had the pleasure of working with an outstanding group of advisors: Jane Goodall, Robert Fry, Toshisada Nishida, Randall Susman, Geza Teleki, Frans de Waal, and Richard Wrangham. We recognize the Wenner-Gren Foundation, the L. S. B. Leakey Foundation, and WBEZ Radio for co-sponsoring the symposium. We especially thank Cecilia Garibay and Kirsten Buckstaff for their skillful help with manuscript preparation. Finally, very special recognition and gratitude are due the contributing authors.

This issue of the *Bulletin* celebrates over 30 years of field work in Gombe and 25 years in Mahale, and recognizes major contributions worldwide to the understanding of chimpanzees and bonobos.

Paul G. Heltne President

Linda Marquardt Managing Editor / Symposium Coordinator

OVERVIEWS

The Importance of Understanding Diversity

Jane Goodall

Director, Gombe Stream Research Centre, Dar Es Salaam, Tanzania

Chimpanzees are rapidly vanishing throughout their range. The destruction of their habitat is increasingly fragmenting the remaining populations. Many of the surviving groups number less than 100 individuals, and genetic diversity in these groups is unlikely to be sufficient to sustain the populations.

It is only as we have gradually accumulated information on a number of different communities of chimpanzees across the species' range in Africa that we have begun to realize the extent to which behavior patterns vary from one area to another. Some variations in behavior have, without doubt, evolved as a direct result of differential environmental pressures. Others, equally certainly, have appeared through processes of cultural evolution similar to those which have led to the staggering diversity of social behaviors that we find in *Homo sapiens*. It is vital that research on wild chimpanzees be initiated in many more parts of their range if we are even to begin to understand the full extent of behavioral flexibility in our closest living relatives. Only then can we begin to tease apart the differential effects of environment and learning.

Explaining Diversity: Ecology and History in the Lives of Chimpanzees

Richard W. Wrangham

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts

Chimpanzees and bonobos have diverse behavioral traditions, as well as substantial variation in their ecology, life-history, social organization, and relationships with other species. The discovery of this variation prompts questions about its significance. How much of the variation is adaptive? To what extent can we attribute it to different sources, such as genetic adaptation, ecological adaptation, behavioral adaptation, demographic perturbations, individual differences, arbitrary traditions, or observer interference? Answers to such questions should help us to define better the evolutionary significance of advanced cognitive abilities.

Chimpanzee Natural History and Its Importance for Understanding the Human Career

Randall L. Susman

Department of Anatomical Sciences, School of Medicine, SUNY at Stony Brook, Stony Brook, New York

Over the past quarter century, chimpanzees, including pygmy chimpanzees, have increasingly occupied center stage in research on the behavior and ecology of the earliest hominids. The importance of the genus *Pan* has been underscored by (1) studies of free-ranging animals that reveal tool-use behavior, hunting, and complex sociality; (2) studies of captive animals that demonstrate advanced cognitive abilities and a close genetic affinity between African apes and humans; and (3) the early hominid fossil record that reveals often close anatomical similarities between chimpanzees and early ape-men.

The importance of chimpanzees for understanding human evolution provides a major impetus for conserving natural populations of these apes in undisturbed environments. If fieldwork is to continue to be relevant to paleoanthropology, then it must be based on truly naturalistic behavioral and ecological data. If present rates of habitat destruction and depredation of the primate fauna continue across sub-Saharan Africa, anthropologists will lose forever the single most important source of data for reconstructing events and behavioral pathways in the human career.

The African Apes: A Review of Behavioral Diversity (Public Session)

Diane Doran

Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina

The African apes – gorillas, chimpanzees, and bonobos (or pygmy chimpanzees) – are similar in their geographic distribution (Africa), phylogeny, relatively large body size, and long life span. In spite of these similarities, there are differences among the three species. Most of our knowledge of gorillas, the largest of the three (weighing up to 400 pounds), comes from studies of the mountain gorillas of the Virunga Volcanoes. Mountain gorillas are folivorous in their diet, live in cohesive groups (< 35), and travel very short distances (approximately 500 meters) each day. Chimpanzees and bonobos are similar to each other and differ from gorillas in their diet (primarily frugivorous), more extensive day ranges, smaller body size, and "looser" fission-fusion type of social organization. Chimpanzees and bonobos live in large communities that regularly split into smaller parties varying in size (from lone animals to an entire community) and composition (e.g., mothers with infants, mixed sexes). There are, however, some striking differences between the two chimpanzee species. Chimpanzees are a male-bonded society, whereas bonobos show strong affiliative relationships between mothers and adult sons and between females. Although both species are primarily frugivorous, bonobos include more herbaceous material in their diets, whereas chimpanzees hunt, kill, and eat monkeys, and in West Africa, use tools to crack open and feed upon nuts.

Behavioral Diversity: The Problem of Comparative Ethography (Workshop Summary)

Jan A. R. A. M. van Hooff

Ethology and Socio-ecology Group, Universiteit Utrecht, The Netherlands

To document behavioral diversity within and between populations, agreement should exist on the units of behavior to be compared and their demarcation and categorization. Behavior can be described at different levels of organization, ranging from molecular morphological patterns to molar functional categories. The level chosen for comparison clearly depends on the research questions and hypotheses. At the level of major morphological units of behavior, there are two main ethographies, by van Lawick-Goodall and by van Hooff (the latter also encompasses a hierarchical categorization that is empirically based on temporal contingencies). Workshop participants felt that it would be relatively easy to come to a standardized ethographic taxonomy; however, it was considered illusory to expect a truly exhaustive standard ethogram for a species with behavior as complex as the chimpanzee.

Variation in behavior also exists at the level of functional organization; comparisons at this level should consider the program rules of behavior (its patterning and contextual contingencies). Agreement should be reached on the empirical criteria for distinguishing functions such as "play," "teasing," "reconciliation," etc. A recommendation was passed to develop a central archive of video ethographies.

SOCIO-ECOLOGY

ECOLOGICAL AND ANATOMICAL PERSPECTIVES ON BEHAVIOR

The Locomotor Behavior of Chimpanzees and Pygmy Chimpanzees

Diane Doran

Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina

Interspecific differences in chimpanzee locomotor behavior were tested to resolve debate over whether there were behavioral correlates to the relatively long and narrow scapula and curved phalanges of pygmy chimpanzees. Quantitative studies of positional behavior in the field were conducted for 12 months on pygmy chimpanzees in the Lomako Forest of Zaire and for 7 months on chimpanzees in the Tai Forest of the Ivory Coast. Results demonstrated that (1) pygmy chimpanzees engage in more arboreal travel than do chimpanzees; (2) during arboreal locomotion, pygmy chimpanzees use more quadrupedalism and less climbing and scrambling, and males, at least, are more suspensory than male chimpanzees; and (3) although both species show similar trends in locomotor development, adult pygmy chimpanzees are more similar to immature rather than mature chimpanzees in their arboreal locomotor behavior. These results demonstrate that there are predictable behavioral correlates associated with the interspecific morphological differences of chimpanzees and pygmy chimpanzees.

Sex Differences in Chimpanzee Positional Behavior, Activity Budget, and Diet

Kevin D. Hunt

Department of Anthropology, Indiana University, Bloomington, Indiana

A yearlong study of the positional behavior of Gombe and Mahale chimpanzees yielded 701 hours of observation. Males spent more time walking than females and walked faster. When apart from males, females spent significantly more time in the trees and among the terminal branches, and more time resting, feeding, and walking between food patches. Although arm-hanging is principally a fruit-eating posture in chimpanzees, males ate a higher proportion of fruit than females and arm-hung less often. Females transferred and squatted more than males; males sat more often. Males had a larger food list, ate more large-tree foods, ate more food found in dense patches, and ate more fruit. Females ate more ants, more small-tree fruits, more blossoms, more seeds, and more leaves. In the presence of males, females ate less fruit, more pith, spent less time in the trees and less time among the terminal branches. These results suggest that females spend more time arm-hanging because social rank differences between males and females force females to utilize small trees and precarious feeding sites, where arm-hanging is the most effective harvesting posture.

Ecological Determinants of Behavior: Comparisons between Lomako and Kibale

Frances J. White

Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina

Colin Chapman

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts

The two species of chimpanzee, *Pan paniscus* and *Pan troglodytes*, differ markedly in social organization. The social system of *P. troglodytes* is characterized by strong affiliation among males and little among females. *P. paniscus*, in contrast, shows frequent affiliation among females, and little among males. *P. paniscus* also shows strong affiliation between males and females. These differences in social system have been attributed to the different levels of feeding competition experienced by each species. While prior studies have compared populations from divergent habitats, this new study of the ecological determinants of behavior of the two chimpanzee species examines equivalent data from study populations in similar forested habitats: *P. paniscus* in the Lomako Forest of central Zaire and *P. troglodytes* of Kibale in Uganda. Data is presented on spatial positioning and nearest neighbor choices in order to compare directly the impact of different ecological conditions on social affiliation in the two species.

Predation by Leopards on Chimpanzees and Its Impact on Social Grouping

Christophe Boesch

Institute of Zoology, University of Basel, Basel, Switzerland

During a five-year period, 29 interactions between chimpanzees and leopards have been observed or inferred in the tropical rainforest of the Taï National Park, Côte d'Ivoire. Chimpanzees chased away leopards in nine cases, rescued alarm-calling chimpanzees in 11 cases (in four of these, footprints or growls of leopards were noted), and nine times leopards attacked chimpanzees, injuring six of them and killing four. Two of the latter chimpanzees were most certainly eaten by the leopard later. Predation by leopards is estimated to be the primary cause of mortality in the Tai chimpanzees, and individual chimpanzees may experience a risk of predatory attack of 0.30 per year. Taï chimpanzees specifically adapt their grouping patterns to food availability and to predation: with abundant food and low predation, party size increases and mixed parties are more frequent, whereas with the same food condition but with high predation, party size decreases and all-male party types increase. Comparisons with data on grouping patterns from Gombe and Mahale chimpanzees living in more open habitats support the hypothesis that this species adapts itself to leopard predation, which is known to be lower in savanna habitats. The grouping patterns of the bonobo in Lomako Forest seem more similar to Taï than to Gombe or Mahale chimpanzees, suggesting an analogous adaptation to high predation pressure.

FEEDING ECOLOGY

Comparative Feeding Ecology of Bonobos, Gorillas, and Chimpanzees

Suehisa Kuroda

Department of Zoology, Kyoto University, Kyoto, Japan

In the Ndoki Forest of the northern Congo, western lowland gorillas and chimpanzees are sympatric. In the fruiting season, both species feed on the same fruits. When fruits become scarce, gorillas rapidly change their main food from fruits to leaves and shoots, whereas chimpanzees continue to seek fruits. Thus, niche separation occurs and direct competition is avoided. Gorillas forage in all types of vegetation, including swamp, and they seem more adaptive to wet vegetations than chimpanzees.

Bonobos are basically frugivorous, and they have several ecological adaptations in common with western lowland gorillas: frequent foraging in swamp vegetation, constant feeding on Marantaceae and aquatic herbs, feeding on earthworms and insects in the ground, and the lack of tool-use for feeding. These characteristics suggest bonobos and gorillas have a long history in the tropical rainforest. By contrast, chimpanzees' adaptation to the drier vegetation in the Ndoki Forest may suggest that their origin is in drier areas.

Implications of Site Differences in Food Selection by Chimpanzees

G. Isabirye-Basuta

Department of Zoology, Makerere University, Kampala, Uganda

Richard W. Wrangham

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts

Foods that are commonly eaten by chimpanzees at one study site may be ignored at another, even when availability is equivalent. Such foods include both general food-classes (such as seeds or bark) and specific food-items (e.g., particular species of fruit). Because such foods often demand complex processing, the principal previous explanation for site differences has been that variation in inventiveness constrains food choices; however, this idea does not explain all cases. Here we examine the role of habitat-wide differences in overall levels of food availability by testing the hypothesis that populations with low levels of food abundance are forced to include lower-quality items in the diet. Although results are somewhat contradictory, most indices suggest that Kibale chimpanzees have more food available than in Gombe or Mahale. This has interesting implications for possible demographic and health differences between sites.

The Relative Importance of Terrestrial Herbs for Bonobos and Chimpanzees: Comparative Data from Lomako and Kibale

Richard Malenky

Department of Anatomical Sciences, SUNY at Stony Brook, Stony Brook, New York, and Lomako Forest Pygmy Chimpanzee Project, Zaire

Richard W. Wrangham

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts

Consumption of terrestrial herbaceous vegetation (THV) has been suggested to be especially important for *Pan paniscus*, and has been invoked to explain differences in their dentition and social organization relative to *Pan troglodytes*. Here we compare distribution and consumption of THV by *P. paniscus* in Lomako Forest, Zaire, and by *P. troglodytes* in Kibale Forest, Uganda. In Lomako, THV is eaten with regularity throughout the year, despite changes in the availability of fruit. It does not appear to promote aggregation into large parties. In Kibale, THV is also eaten throughout the year, and consumption increases during periods of fruit shortages. Weights of fibrous materials in dung indicate that THV constitutes a greater proportion of the diet in Lomako than in Kibale. We examine the implications of these data for the biology and the behavior of both species of *Pan*.

Eating a Dead Colobus Monkey (Video Presentation)

Christopher Boehm

Department of Anthropology, University of Southern California, Los Angeles, California

In this video, Gombe field assistants place a colobus monkey, fatally wounded by chimpanzees, where the chimpanzees will find its corpse the following morning. Adult male Atlas cannot cope with this potential source of food, but Gremlin and her mother, Melissa, begin to eat it. When Atlas joins them, the agonistic behavior that frequently accompanies eating and sharing of meat is notably absent. It is hypothesized that when meat is not fresh, and when the hunting experience is not recent, agonism is reduced. The calmer style of sharing can be compared with descriptions of highly cooperative meat-sharing from the Taï Forest.

Hunting Scenes of Mahale M Group Chimpanzees (Video Presentation)

Hiroyuki Takasaki

Center for African Area Studies, Kyoto University, Kyoto, Japan

These video scenes present the general pattern and process of red colobus monkey hunting by M Group chimpanzees at Mahale Mountains in western Tanzania. The scenes were selected from 45 hours of videotaped behavior taken by H. Takasaki between March 1987 and December 1988 (41 hours) and in July and August 1991 (4 hours).

Food-Related Behavior in Bonobos (Video Presentation)

Amy Parish

Department of Anthropology, University of California, Davis, California

Sexual behavior among bonobos occurs almost invariably in situations involving food. The video presents feeding scenes from the San Diego and Stuttgart zoos. Dominant females often sit in the midst of food clumps, and other individuals approach, make sexual presentations, and often engage in sexual activity before obtaining food. Individuals solicit same- and opposite-sex partners for sex when food is introduced or even in sight. Scenes are presented in which males exchange bundled food for sex with a female. It is hypothesized that sex performs a tension-reduction function during feeding, and that food can be the basis for sex-for-food exchanges between males and females.

TOOL USING

Tools Compared: The Material of Culture?

W. C. McGrew

Scottish Primate Research Group, University of Stirling, Stirling, Scotland

Increasing knowledge of wild chimpanzees, *Pan troglodytes*, shows a rich diversity of tool use. At least 32 populations use tools in east, central west, and far west Africa. Though not all populations are proven tool users, this widespread occurrence suggests species-typicality. Habitual tool use is known for at least 12 populations, and most of the 19 known behavioral patterns are used in subsistence. No type of tool use is universal, nor does any single population show more than a fraction of the species' repertoire. Regional variations exist, e.g., only far western (but not eastern nor central western) chimpanzees are known to open nuts with hammers. Technological traditions differ across populations, but terming these as cultural adds nothing in explanation. It remains to be seen whether or not "true" imitation or teaching occurs in the transmission of tool use.

Nut-Cracking Behavior and Environment at Bossou

Tetsuro Matsuzawa

Department of Psychology, Primate Research Institute, Kyoto University, Aichi, Japan

Yukimaru Sugiyama

Primate Research Institute, Kyoto University, Aichi, Japan

Nut-cracking behavior in wild chimpanzees using natural stone hammers and anvils was studied through experimental analysis at Bossou, Guinea. Oil-palm nuts and stones were prepared at an experimental site in the chimpanzees' ranging area. The stone-tool use was directly observed and video-recorded. The chimpanzees show perfect laterality in hand-use at the individual level, but no left-right bias at the population level. Each of the chimpanzees has its own favorite stones. An old female chimpanzee showed an example of meta-tool-use behavior, in which one anvil stone was placed on another anvil stone in order to keep the surface flat. The details of stone-tool use are described with a videotape.

At the Roots of Objectivity: Termite Fishing in Chimpanzees (Video Presentation)

I. Eibl-Eibesfeldt

Laboratory of Human Ethology, Max Planck Institute, Andechs, Germany

When fishing for termites, chimpanzees demonstrate persistence and patience. Temper tantrums may occur in frustrating situations (as demonstrated by Sultan's temper tantrum in Köhler's experiment); however, they were not observed in the termiting context. It appears that the need for voluntary motor control has selected for decoupling motor patterns from agonistic emotions. In higher mammals, play behavior is also characterized by lack of or dampened agonistic arousal (even though the motor patterns of fighting may be playfully employed). It is hypothesized that the continued evolution of tool using in protohominids and man (which may have brought about such decoupling as right-handedness and lateralization of the brain) further enhanced the capacity to separate emotions from voluntary motor control. This capacity for decoupling eventually extended to speech and thought processes (internalized action), and thus paved the way for " objectivity" in mental processes and actions. In other words, objectivity had its roots in object manipulation.

Tool-Using Scenes of Mahale M Group Chimpanzees (Video Presentation)

Hiroyuki Takasaki

Center for African Area Studies, Kyoto University, Kyoto, Japan

These video scenes of tool use show fishing for wood-boring *Camponotus* ants, which is often performed by Mahale chimpanzees, and leaf sponging behavior, which is rarely observed. The

scenes were selected from 45 hours of videotaped behavior of the M Group chimpanzees at Mahale Mountains in western Tanzania, filmed by H. Takasaki between March 1987 and December 1988 (41 hours) and in July and August 1991 (4 hours).

Bonobo Tool-Using Behavior (Video Presentation)

Suehisa Kuroda

Department of Zoology, Kyoto University, Kyoto, Japan

Tool-using behavior to obtain food is rarely seen in bonobos (pygmy chimpanzees) under natural conditions. This does not mean that they lack such abilities. Patrick Neary recorded spontaneous tool-using behavior in young bonobos at the San Diego Zoo. In the wild, the richness of the habitat and the bonobo's strong orientation to social concerns may make the development of such behavior unnecessary.

Two Methods of Dipping for Army Ants (Video Presentation)

Christopher Boehm

Department of Anthropology, University of Southern California, Los Angeles, California

Chimpanzees at Gombe feed on termites and army ants, while those at Mahale feed on several ant species but not on army ants. It is hypothesized that these biting ants could have been so aggressive at Mahale that no cultural tradition of feeding on them arose, whereas the Gombe chimpanzees cope by creating long wands that enable them to feed from a distance. The video footage shows a Gombe adult female fishing for army ants with a short tool normally used for termites, which brings her too close for comfort. She retreats to fashion a longer, rigid wand that allows her to dip for the army ants from a distance.

Tool Using

See also Cognition (Ingmanson)

Nest Building

See Research Site Overviews (Fruth and Hohmann, Sept et al.)

SOCIAL RELATIONSHIPS

FIGHTING AND RECONCILIATION

Food-Sharing, Reciprocity, and Moralistic Aggression in Chimpanzees

Frans B. M. de Waal

Department of Psychology and Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia

Two captive groups of chimpanzees (Pan troglodytes) were studied to document a wide range of beneficial and harmful acts. Sharing of plant foods, coalition formation, grooming, negative interventions, and aggressive behavior were symmetrically distributed over the adult matrix, i.e., the rate with which individual A directed a particular behavior towards B correlated with the rate of the same or another behavior directed by B towards A. Reciprocity existed in the exchange of social favors; turn-taking that prevents a one-sided accumulation of benefits; delayed retaliation against aggressors; and rejection of food requests by "stingy" individuals. Because kinship can be excluded, and because various analyses complement and support one another, a coherent picture emerges of sophisticated mechanisms of reciprocity in both the positive and negative domains of chimpanzee social life. Some of these mechanisms relate to human systems of morality and justice in that they appear to serve retribution and the enforcement of reciprocity rules.

Competition, Cooperation, and Tension Regulation in a Community: Ethological Studies at the Arnhem Chimpanzee Consortium

Jan A. R. A. M. van Hooff

Ethology and Socio-ecology Group, Universiteit Utrecht, The Netherlands

The Arnhem Chimpanzee Consortium has existed for exactly 20 years. The consortium was set up as a pioneering attempt to create a pseudo-natural social situation. It houses between 20 and 30 chimpanzees, among which there have always been a couple of grown males. This situation has enabled us to monitor social processes in detail and with a consistency that is not easily realized in nature. Research has focused on the social processes by which individuals regulate their position in the community, particularly on the relationships between the adult male members of this male-bonded species. The processes by which social homeostasis is achieved (conflict and tension regulation) have received special attention. The research demonstrates that studies on the social behavior of captive apes, given adequate and representative conditions, can contribute in essential ways to our understanding of the principals of behavioral and social organization.

Conflict Interactions among Male Chimpanzees at Mahale (Film and Discussion)

Shigeo Uehara

Faculty of General Education, Sapporo University, Sapporo, Japan

Usurpation of alpha status by males has been observed only rarely during the course of long-term field studies (1965 to present) on habituated chimpanzees in the Mahale Mountains, Tanzania. In May 1976 the alpha male, Kasonta, of the small-sized K Group, was displaced by the beta male, Sobongo, who was supported by the third-ranking male, Kamemanfu. After the rank reversal, Kasonta spent much of his time alone, but in September 1977 he suddenly resumed traveling with K Group. Assisted by Kamemanfu, Kasonta regained stable status and mating opportunities in the group until January 1978, while Sobongo became peripheral after November 1977.

Another male, Kajugi, of the large-sized M Group, lost his alpha status in June-July of 1978. He was intermittently seen until April 1982, mostly alone or on several occasions with some adult males, but he was never seen in the vicinity of the new alpha male, Ntologi. Kajugi probably failed to receive constant support from any particular males against Ntologi. The formation of effective alliances seems crucial for a defeated alpha male to maintain a stable position in the male rank order, particularly in relation to the new alpha male

Triadic Interventions (Video and Discussion)

Christopher Boehm

Department of Anthropology, University of Southern California, Los Angeles, California

Primatologists have encountered difficulties trying to interpret what is going on when, for example, an alpha male hears a fight developing and races to the spot to end the fight. Thus, while the dyadic peacemaking interactions of chimpanzees have been very well interpreted by Frans B. M. de Waal as to proximate cause, the interpretation of triadic interventions remains in some doubt; indeed, it has been mainly for the macaques (whose triadic interventions are relatively frequent) that such behaviors have been variously interpreted as involving strategies of alliance building or of improvement of individual dominance standing through intimidations. In *The Chimpanzees of Gombe*, Jane Goodall (discussing only chimpanzees) characterizes the immediate causes of such interventions as "stopping aggression/emphasizing rank/restoring social harmony/protecting both combatants." Thus, the proximate causes for triadic intervention might involve one or more of these strategies. This, by itself, makes cross-group comparison rather problematic. Cross-group comparison is further complicated by the sheer variety of tactics (illustrated in the video) that accompany the cluster of basic strategies.

Reconciliation Patterns among Newly Introduced Captive Chimpanzees (Video and Discussion)

Kate Baker

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Susan McDonald Black

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Barbara Smuts

Departments of Psychology and Anthropology, University of Michigan, Ann Arbor, Michigan

Females in the newly established social group at the Detroit Zoo invested more energy in reconciling with each other than did females in a settled social group. Female-female reconciliations were more intense than female-male reconciliations. Since reconciliations are thought to reflect a need for stabilization and tension reduction, these results suggest that the female-female sphere at the newly formed Detroit Colony was more active in terms of aggression, hierarchical relationships, and tension reduction than the female-female sphere is thought to be in general.

Fighting and Reconciliation (Video Presentation)

Toshisada Nishida

Department of Zoology, Kyoto University, Kyoto, Japan

The former alpha male of M Group was dethroned in March 1991. In August, the new alpha male, Kalunde, had three rivals: second-ranking Shike, third-ranking Nsaba, and a young adult male, Jilba. Agonistic confrontations occurred daily among adult males. Jilba never pant-grunted to Kalunde or to other adult males except Shike. Moreover, Jilba often attacked adult females without apparent reason. On August 29, Jilba challenged Kalunde while in a tree, and kicked him. After that, Jilba was chased away by Kalunde. On the next day, Jilba and Kalunde apparently reconciled, engaging in a prolonged bout of mutual grooming. However, on October 7, Jilba was the subject of a gang attack by Kalunde, five other adult and adolescent males, and two adult females. Kalunde held Jilba on his back while other chimpanzees, one after another, bit his legs, arms, and back. However, Jilba was not killed. This is the first record in which a gang attack was directed toward an in-group member other than an ex-alpha male. This may have been a consensus-based punishment directed at a bad-mannered young male.

Fighting and Reconciliation (Video Presentation)

Frans B. M. de Waal

Department of Psychology and Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia

The following scenes were observed of bonobos at the San Diego Zoo. Male-male: (1) various reassurance gestures, including assertive chest knocking; (2) hold out hand, chest knocking, penis-touch; (3) food competition, followed by embrace; (4) shake wrist, chest knocking, genital inspect: (5) moat incident, ending with chest knocking, followed by scrotum rubbing. Female-female: (1) raisins fight, followed by GG-rubbing; (2) sugar cane competition, followed by brief GG-rubbing in slow motion.

Fighting and Reconciliation in Bonobos (Video Presentation)

Takayoshi Kano

Primate Research Institute, Kyoto University, Aichi, Japan

Among bonobos, severe fights, which result in serious wounds for one or more participants, are rarely observed in either intragroup or intergroup conflict. Adult males are the principal participants in aggressive interactions. Adult females are not clearly subordinate to adult males. On the contrary, dominant females are respected by and can threaten adult males. Reconciliations take the form of sex-like behaviors such as genito-genital rubbing, rump-rump rubbing, and mounting. These behaviors frequently occur immediately following aggressive conflict, which occurs more often over food than over mating.

MOTHER-INFANT BEHAVIOR

Weaning Conflict in Chimpanzees

Toshisada Nishida

Department of Zoology, Kyoto University, Kyoto, Japan

Weaning conflict is one of the most interesting aspects of chimpanzee behavior. An infant that is faced with strong maternal rejection for the first time in its life displays various responses to the mother's weaning behaviors. During this intense period of conflict, which lasts more that six months and corresponds with the mother's resumption of post-partum estrus, the infant develops social tactics that will be useful in later social interactions with group members other than the mother. For

example, during weaning, an infant begins to groom its mother frequently, uses subtle tactics to gain access to the mother's nipples, and uses exaggerated tactics such as temper tantrums to induce the reluctant mother to comply with its requests.

Mother-Infant Behavior

Jane Goodall

Director, Gombe Stream Research Centre, Dar Es Salaam, Tanzania

Thirty-one years of field data on mother-infant behavior in the Gombe chimpanzees has presented us with a staggering amount of information. Regrettably there has been, as yet, no systematic analysis of these data, although this is planned in the near future.

Maternal techniques differ widely between females. Daughters learn certain patterns from their own mothers and other patterns as a result of experience gained raising successive offspring. The effects of early experience are often clearly revealed in adult life. The strength of long-term bonds between family members has been known for some time. During recent years we have been able to collect new information on the behavior of orphans following the deaths of their mothers and the extent to which "maternal" behavior may be released in relatives of either sex and even, on occasion, in individuals who do not appear to be closely related by blood.

The Adoption of Two Orphaned Chimpanzees at the Detroit Zoo (Video Presentation)

Susan McDonald Black

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Kate Baker

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Two two-year-old orphaned female chimpanzees were integrated into a large captive colony (which included eight adults and one juvenile) at the Detroit Zoo. The successful integration of the two infant chimpanzees into the colony was influenced by (1) early introduction to the foster mothers (through plexiglass, then wire mesh, then physically) and (2) five months spent in a nursery group (with the two foster mothers and a juvenile female) learning appropriate chimpanzee social skills before introduction to the larger group.

Mother-Infant Scenes of Mahale M Group Chimpanzees (Video Presentation)

Hiroyuki Takasaki

Center for African Area Studies, Kyoto University, Kyoto, Japan

Video scenes include experienced and inexperienced nursing mothers, transportation postures, baby-sitting, an unsuccessful adoption and a successful adoption, temporary adoption of a lost infant by a passerby, transportation of a dead infant by its mother, and grooming between a mother > 50 years old and her 35–year-old offspring.

SOCIAL RELATIONSHIPS

Effect of a Mother's Death on Her Offspring's Social Relationships with Group Members: Bonobos at Wamba, Zaire

Takayoshi Kano

Primate Research Institute, Kyoto University, Aichi, Japan

After the disappearance of an old female (Kame), her two adult sons' (Mon and Tawasi) associations with other group members fell drastically, while her juvenile daughter (Tosi) maintained a high association rate by switching to another old female (Mitu). This allomother-like association was the result of Tosi actively approaching and following Mitu, and Mitu's "indifferent tolerance." Familial interactions dropped to almost zero. Aggression by Kame's offspring decreased, while aggression toward them increased. Females were more tolerant of Kame's orphans than males. Those individuals who had been more familiar with Kame in the past were also more tolerant than those who had spent less time associating with her.

We can conclude that (1) a mother's death severs the bond among siblings, (2) a mother's death influences the social status of her sons, and (3) close associations with adult bonobo females may provide juvenile orphans with a source of allomothers.

VOCALIZATION

Dialects in Wild Chimpanzees?

John C. Mitani

Department of Anthropology, and Evolution and Human Behavior Program, University of Michigan, Ann Arbor, Michigan

Toshikazu Hasegawa

Department of Psychology, Teikyo University, Tokyo, Japan

Julie Gros-Louis

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Peter Marler

Department of Zoology, University of California, Davis, California

Richard Byrne

Scottish Primate Research Group, Department of Psychology, University of St. Andrews, St. Andrews, Scotland

Chimpanzees emit a loud, species-typical long-distance call known as the pant hoot. Geographic variation between the pant hoots of chimpanzees living in two neighboring populations (in the Mahale Mountains National Park and Gombe Stream National Park, Tanzania) was examined. Analysis of six acoustic features revealed subtle differences in the way chimpanzees from the two populations called. Individuals from the Mahale study site uttered one section of their pant hoots at a faster rate and with shorter elements than animals from Gombe Stream. In addition, individuals at Mahale delivered broader-band, higher pitched "climax" elements than males from Gombe. While genetic factors, anatomical differences, variations in the use of calls at the two sites, and changes in calling over time may account for variability between populations, we suggest the additional possibility that differences in pant hooting may be due to learning.

Rank Differences in Vocal Production of Kibale and Gombe Chimpanzees as a Function of Social Context

Adam P. Clark

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Wild chimpanzee vocal behavior was investigated during an 18-month study of habituated, unprovisioned chimpanzees in the Kibale Forest, Uganda. Vocalization rates were calculated according to whether individuals were alone, with females, or in mixed parties. Adult females and low-ranking adult and subadult males were quiet except in mixed parties, whereas high-ranking

males vocalized in all social contexts. These results were compared with published data from the Gombe provisioning area. Vocal production at Gombe resembled that of mixed parties at Kibale. These observations emphasize the importance of social context in determining patterns of vocal behavior, and suggest that the provisioning area at Gombe resembled a natural socioecological context occurring at large fruiting trees.

The functional significance of uttering pant hoots at fruiting trees was examined. Contextual analysis revealed the following: (1) pant hoots were given exclusively by high-ranking males at trees that did not already have chimpanzees present ("empty trees"); (2) compared with quiet arrivals, arrival parties that pant hooted were not joined by new parties more frequently; (3) high-ranking males called at empty trees regardless of the amount of fruit remaining; and (4) high-ranking males called regardless of the presence of their closest associates. Thus, pant hooting on arrival appeared to be a marker of status, but did not have an obviously attractive effect.

SEXUAL BEHAVIOR

Development and Change in the Social Role of Bonobo Sexual Behavior

Takeshi Furuichi

Laboratory of Biology, Meiji-Gakuin University, Yokohama, Japan

Chie Hashimoto

Primate Research Institute, Kyoto University, Aichi, Japan

Development of genital contact behavior and copulatory behavior was studied in a wild group of bonobos at Wamba. Bonobos begin to engage in genital contact and pseudocopulation at the age of two years. They show wide varieties of genital contact, but these behaviors do not relate to specific social roles. Male infants show a greater interest in adult sexual activity than female infants do. At the age of about five years, females become socially isolated, and by seven to nine years of age, they transfer to other groups. Males continue to stay with their mothers but become much less involved in sexual behaviors. Upon reaching adulthood, both males and females resume frequent display of genital contact and copulatory behavior. The sexual behaviors tend to be fixed in certain patterns and play important social roles such as reducing mental strain, serving as greetings at encounters or approaches, settling agonistic interactions, and forming intimate relationships.

Copulatory Behavior of Pan paniscus, Lomako Forest

Nancy Thompson-Handler

Department of Anatomical Sciences, SUNY at Stony Brook, Stony Brook, New York, and Lomako Forest Pygmy Chimpanzee Project, Zaire

Under totally natural conditions in the Lomako Forest, copulation is relatively infrequently observed. Sexual contact occurs primarily under special circumstances in favored food patches when parties of greater-than-average size gather. Under such special circumstances, social factors may override reproductive physiology. When sexual activity is analyzed by female reproductive classes based on age, parity, and likelihood of fertility, bonobo copulatory behavior appears to deviate less strongly from a chimpanzee-like pattern than previously reported. The greatest exception to this rule is the class of young adolescent females, who are sexually active during all phases of the swelling cycle. These results are discussed in relation to the reproductive biology and life history patterns of the two species of *Pan*.

Nonreproductive Sexual Behavior in Bonobos (Video Presentation)

Amy Parish

Department of Anthropology, University of California, Davis, California

The video illustrates the full repertoire of sexual positions (ventro-ventral, dorsal, upright, opposite), partner combinations (dyads and triads involving combinations of males, females, and immatures), and sexual activities (intercourse, genito-genital or GG-rubbing, oral sex, tongue kissing, masturbation) of bonobos in the San Diego and Stuttgart zoos. Several scenes show males interfering with female sexual interaction. Females "sneak" GG-rubbing while males are out of sight. Bonded females sometimes cooperate to keep food from males. It is hypothesized that males try to discourage female sexual interaction, which may be part of bond formation.

Sexual Behavior See also Feeding Ecology (Parish)

PLAY

Play Scenes of Mahale M Group Chimpanzees (Video Presentation)

Hiroyuki Takasaki

Center for African Area Studies, Kyoto University, Kyoto, Japan

Video scenes include play between immatures, mother-offspring play, play between an immature and an adult male, and play involving objects. Included in the last category are a solo performance using a fruit, and transfer of a fruit from a juvenile brother to an infant sister as an invitation to play.

Play Behavior (Video Presentation)

Christopher Boehm

Department of Anthropology, University of Southern California, Los Angeles, California

The video illustrates typical juvenile play at Gombe, in which expression of agonistic behavior (as well as its inhibition) is developed.

Play among Unfamiliar Adult Chimpanzees at the Detroit Zoo (Video Presentation)

Kate Baker

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Susan McDonald Black

Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Observations of newly introduced chimpanzees during the formation of the Detroit Zoo colony in Michigan revealed unexpected and innovative patterns of play. Females incorporated play in dyadic physical introductions, female-female reconciliations, and in other contexts of social tension. They played at relatively high rates throughout the six months after group formation, especially during periods of crowding. These results suggest that play performed a tension-regulating function among females in the Detroit Zoo colony.

Play-Initiation Gestures of Young Chimpanzees (Video Presentation)

Michael Tomasello

Department of Psychology and Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia

Young chimpanzees solicit play from one another with a wide variety of gestural signals. In a longitudinal study of a captive group of chimpanzees, we found that individuals produce these signals intentionally. This intentionality is clear because in the process of producing these signals they either (1) alternate their gaze between interlocutor and goal, or (2) wait for a response. Intentionality is also clear from the fact that an individual may use the same signal for several goals and different signals for the same goal. Young chimpanzees acquire intentional signals by a process of conventionalization, not by strictly defined imitative learning.

Play
See also Group Specific Behavior (de Waal, van Hooff)

GROUP SPECIFIC BEHAVIOR

Group Specific Behavior: Mahale (Video Presentation)

Toshisada Nishida Department of Zoology, Kyoto University, Kyoto, Japan

The following behaviors of Mahale chimpanzees have rarely, if ever, been reported from other sites in Africa. The "grooming-hand-clasp" is not seen at Gombe, but was reported from Kibale. "Ground grooming" is displayed by only two young adult males of M Group as a displacement activity performed in a tense situation. For example, a young male, Jilba, grooms dry leaves on the ground while being groomed by the alpha male. "Leaf-clipping" is a frequently observed courtship display. During the "cushion-and-stamp courtship display," a male chimpanzee bends one to several shrubs or herbs to the ground and stamps on them with one foot while facing an estrus female. Adult males "throw stones into running water" as a component of their charging displays. Stone throwing is typically repeated again and again. Most of the stones fall into the water. The splashing sound has a great intimidating effect on other chimpanzees.

Intergroup Encounter of Bonobos in a Natural Forest (Video Presentation)

Takeshi Furuichi

Laboratory of Biology, Meiji-Gakuin University, Yokohama, Japan

This is the first film of an intergroup encounter of bonobos in a natural forest. As reported for encounters at artificial feeding sites, two groups approached each other while exchanging vocalization and initially showed excited display behavior. However, their excitement gradually lessened, and they showed familiar behaviors such as genital contact, co-feeding, grooming, and copulation with members of the other group. Although males tended to stay behind the front line, females easily mixed at the boundary area.

Group Specific Behavior (Video Presentation)

Frans B. M. de Waal

Department of Psychology and Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia

The following scenes were observed of bonobos at the San Diego Zoo and of chimpanzees at the Yerkes Field Station. (1) Blindman's Bluff (juvenile bonobos): Lana with fingers in eyes; Akili swings in rope; Akili with arm over eyes. (2) Funny Faces (juvenile bonobos): several faces, chattering; lower lip in; upper lip out. (3) Groom Postures (juvenile bonobos): foot/hand clapping; chest beat, clapping; foot clapping; hands/feet clapping; mutual chest beat. (4) Miscellaneous (chimpanzees): groom posture; sand-throwing during greeting.

Behavioral Diversity in Solitary Play at Arnhem (Video Presentation)

Jan A. R. A. M. van Hooff

Ethology and Socio-ecology Group, Universiteit Utrecht, The Netherlands

Behavioral diversity between and within chimpanzee populations may occur at several levels of behavioral organization. Diversity may be the result of locality-specific forces (such as the availability of certain food resources, commodities, and implements). Thus, different traditions develop as a result of a selective process on behavior, reinforced by principles of functional effectivity and efficiency. The development of fads and fashions is constrained by these functional demands.

Play (particularly autoplay and certain forms of exploratory behavior) offers more freedom for non-functional and random variation and, therefore, for the study of how social factors shape behavioral fashions and how behavioral fashions spread, fixate, and disappear. The film fragment from Bert Haanstra's *The Family of Chimps* shows the rich diversity of solitary locomotor and manipulative play patterns existing in the Arnhem Zoo chimpanzee colony and conveys the scope which this category of behavior offers for the study of intra-group variation.

COGNITION

Language from Pan to Man

Sue Savage-Rumbaugh

Department of Biology, Georgia State University, and Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia

Language acquisition by apes has been a controversial topic, mainly because previous research has focused upon what apes can say rather than what they can understand. More recently, an approach which focuses upon apes' natural understanding of normal human speech has produced results that are both striking and easily understandable by English-speaking persons. Apes do not have the vocal apparatus to produce speech; consequently, their language acquisition abilities are best revealed by their capacity to understand words and sentences rather than to speak them. Recent work with bonobos indicates that they learn to comprehend spoken language when exposed to it in the context of normal daily living. Their language comprehension skills are comparable to that of a two-year-old child and include the ability to understand new sentences on first presentation and to produce simple grammatical constructions.

Contributions from Studies of Cognition to Chimpanzee Conservation: Numerical and Inferential Processes

Sarah T. Boysen

Primate Cognition Project, Department of Psychology, Ohio State University, Columbus, Ohio

Studies of cognitive processes in captive chimpanzees, particularly over the past two decades, have contributed significantly to our understanding of the information-processing capabilities of apes. We are currently pursuing detailed studies of the emergence of numerical competence, including rudimentary summation, subtraction and representational skills with symbols, and studies of inferential processes in chimpanzees. These studies, as well as work from other cognitive laboratories, appeal to the scientific community because they add to our understanding of the evolution of cognition. Studies of ape cognition can also provide the public with a greater understanding of the social and intellectual capacities of the chimpanzee, raise awareness concerning efforts to establish protected sites in Africa, enhance captive housing and enrichment efforts, and serve as a powerful mechanism for educational outreach on the plight of chimpanzees in both captivity and the wild.

Why Do Chimpanzees Attribute Mental States to Others?

Daniel Povinelli

New Iberia Research Center and Department of Anthropology, University of Southwestern Louisiana, New Iberia, Louisiana

Lucian Hughes

Department of Computer Science, Yale University, New Haven, Connecticut, and Institute for the Learning Sciences, Northwestern University, Evanston, Illinois

A variety of lines of evidence now suggest that chimpanzees possess a theory of mind. That is, they behave as if they are capable of reasoning about the mental experiences of other individuals. We describe recent experimental data suggesting that chimpanzees understand the causal connection between *seeing* and *knowing*. In addition, we describe ongoing research which explores the chimpanzees' meta-awareness of their own knowledge states. Comparable data from three- and fouryear-old children and rhesus monkeys are also discussed to highlight the nature of the chimpanzees' performance. We compare these results with recent computer simulations of chimpanzee political societies in which chimpanzees do not reason about mental states per se, but nonetheless show robust behaviors which mirror real societies. Given this array of data, we specify the conditions under which chimpanzees might reason about mental states in day-to-day interactions with each other.

Ai: The Chimpanzee Mind (Public Session)

Tetsuro Matsuzawa

Department of Psychology, Primate Research Institute, Kyoto University, Aichi, Japan

I have studied the cognitive behavior of chimpanzees in captivity and in the wild. Ai, the main subject of 13 years of captive research, learned a language-like skill to name numbers, colors, objects, and other aspects by visual symbols. Using the same test method, the perceptual and cognitive abilities of chimpanzees were directly compared with human subjects. The research revealed similarities and differences between the cognitive functions of chimpanzees and humans. The abilities corresponding to Ai's performance were also studied in the wild chimpanzees of Bossou, Guinea. These chimpanzees used stone tools in sophisticated nut-cracking behavior.

Perception and Cognition from the Perspective of Comparative Cognitive Science

Tetsuro Matsuzawa

Department of Psychology, Primate Research Institute, Kyoto University, Aichi, Japan

The cognitive abilities of chimpanzees were directly compared with those of humans in the same test apparatus, following the same test procedure. There were no fundamental differences between the two species in color perception, form perception, and visual acuity. However, there were some differences in the higher order levels of cognition such as individual recognition, cognition of related figures, and pattern recognition. The main subject of the research, the chimpanzee Ai, can label up to the number ten and has learned various symbols for describing the visual world. A summary of the Ai-project and the numerical and linguistic skills shown by the chimpanzee are reported.

Private Signing and Imagination

Roger S. Fouts

Chimpanzee and Human Communication Institute, Central Washington University, Ellensburg, Washington

Deborah H. Fouts

Chimpanzee and Human Communication Institute, Central Washington University, Ellensburg, Washington

Mary Lee Abshire

Chimpanzee and Human Communication Institute, Central Washington University, Ellensburg, Washington

Mark Bodamer

Chimpanzee and Human Communication Institute, Central Washington University, Ellensburg, Washington

Recent research using a remote video recording technique is presented describing chimpanzees' use of private signing and imaginary play behavior. In the private signing studies, 101 hours of video tape were analyzed and 458 instances of private signing were recorded. These instances were classified into the same 11 functional categories that have been used to categorize human private speech. Similar to the findings with humans, a few of the categories accounted for the majority of instances. In the study of imaginary play, 15 hours of video tape were analyzed, and six instances of imaginary play were recorded and classified into two categories of imagination: animation and substitution. These behaviors were compared to analogous behaviors in humans. Finally, some observations are presented that indicate chimpanzees may be capable of temporal seasonal perceptions.

Tool Use among Bonobos in the Wild and the Social Dimensions of Intelligence

Ellen J. Ingmanson

Primate Research Institute, Kyoto University, Aichi, Japan

Tool use and object manipulation have long been used as one indication of intelligence in non-human primates. Since 1987, I have been collecting field data on these behaviors for the bonobos at Wamba. Objects are manipulated by bonobos in many ways and are incorporated into a variety of behaviors. Some of these instances represent tool use. For example, bonobos use objects as tooth picks, fly swatters, "napkins" for wiping, and rain hats. One of the most interesting forms of tool use which I observed is branch dragging to assist in maintaining group cohesion. With this behavior, the bonobos communicate very specific information concerning intention and direction of movement. I have never observed instances in the field of bonobos using tools in food acquisition (in contrast to *Pan troglodytes*). Tool use is a mechanism for solving problems. The problems bonobos must solve in their natural habitat are apparently not related to food acquisition, but involve controlling and manipulating social relations. It is in this realm that we see the greatest complexity in bonobo behavior, including the use of tools. This suggests that bonobo intelligence may be focused in very different directions than that of *P. troglodytes*, with selection having emphasized the social dimension.

Comparing the Ontogeny of Symbol Use in Pan paniscus and Homo sapiens

Patricia M. Greenfield

Department of Psychology, University of California, Los Angeles, California

Sue Savage-Rumbaugh

Department of Biology, Georgia State University, and Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia

The goal of this paper is to describe and place in comparative perspective the conversational and grammatical skills of bonobos exposed to a humanly devised symbol system and to human conversational partners. Kanzi and Mulika, raised at the Language Research Center in Atlanta, Georgia, can express conversational functions such as agreement, choosing between alternatives, and requesting, just as young human children and adults do. In the domain of grammar, Kanzi has constructed meaningful three-element sentences through the logical combination of binary symbolic relations. These structures reflect Kanzi's creativity at the semantic and syntactic levels. They do not reflect the models to which Kanzi has been exposed. These sentence patterns resemble the most frequent "complex" structures invented by deaf children of hearing parents. Kanzi has also produced a few three-symbol combinations that have two levels of constituent structure. This level of hierarchical complexity corresponds to the maximum level of hierarchical complexity reported in chimpanzee tool construction and tool use. Young children show similar correspondences. These cross-species and cross-domain parallels suggest the co-evolution of language and tools going back millions of years to the common ancestor of *Pan* and man.

Comparison of Imitative Learning by Chimpanzees, Educated Chimpanzees, and Human Children (Video Presentation)

Michael Tomasello

Department of Psychology and Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia

In this study, Sue Savage-Rumbaugh and I directly compared the imitative skills of chimpanzees raised in a human-like cultural environment to those of children and non-educated chimpanzees. We found that non-educated chimpanzees copied a human demonstrator's precise actions on only a very few occasions, whereas the performance of the educated chimpanzees and human children was much better (and essentially equal). We conclude that the process by which educated chimpanzees are socialized and enculturated by humans has a profound effect on their ability to focus attention on people and objects, which in turn leads to more human-like skills of imitative learning.

Cognition, Consciousness, and Their Adaptive Significance (Discussion Introduction)

Jan A. R. A. M. van Hooff

Ethology and Socio-ecology Group, Universiteit Utrecht, The Netherlands

The studies reported during this symposium demonstrate increasing sophistication of laboratory experiments on chimpanzee cognition. To what extent do chimpanzees have knowledge of their own functioning, their place in and their relationship with their environment, and the intentional nature of their conspecifics? These questions are opening up more and more to objective empirical research. It is becoming clear that much is still to be learned about the way in which these competencies are used in the wild and where they are of systematic and critical importance to evolutionary development.

The ability of chimpanzees to "see through the eyes of others" and know what others can see and know and thus what others might want to do (suggested by the experiments of Premack, Woodruff and, now, Povinelli) may, for instance, be used advantageously in the cooperative hunting observed in the wild by Boesch. Are there indications that the coordination involved in cooperative hunting is of a different nature than that encountered in other species (such as the baboons of Strum, or other social carnivores)?

CONSERVATION ISSUES IN AFRICA

OVERVIEWS

Problems of Chimpanzee Conservation and Care in Africa

Jane Goodall

Director, Gombe Stream Research Centre, Dar Es Salaam, Tanzania

African countries are economically poor. Conservation attempts must take into consideration the economic needs of the governments and of the people who live in or around the areas in need of protection. Tourism, aid money for rural development, medical help, and conservation-education programs are all vital. So, too, is the in-depth involvement of the people closest to the area to be protected (for example, the field staff at Gombe are involved in data collection and video camera use).

Conservation-education programs are of great importance to captive chimpanzee populations as well. Because of economic poverty, chimpanzees in African zoos are usually not well cared for.

Chimpanzee Conservation: Actions and Options

Geza Teleki

Chairman, Committee for Conservation and Care of Chimpanzees, Washington, D. C.

Ongoing assessments of chimpanzee populations in Africa indicate that the species continues to face crippling pressures from habitat degradation and human persecution. With minor adjustments to the 1987 map of national population estimates, upwards in some cases and downwards in others, the total number of chimpanzees remains at about 175,000 for the continent. In 1991, a new "Action Plan for Chimpanzee Conservation in Africa" serves as a template for setting priorities to guide international sponsorship of field projects. A summary of current and future projects is provided. A new ChimpArk program, focusing on salvage of captive chimpanzees, is described. As an introduction to special reports on these and other topics scheduled for the conservation sessions, trends in international trade and advances in protective legislation are covered. The primary goal is to present an overview of current survival problems and to identify actions that have maximum impact on staving off species extinction.

Impact on West African Chimpanzee Populations of Poaching for the Live Trade

Margery L. Oldfield

Department of Biology, Trinity University, San Antonio, Texas

Simulation results from a dynamic model of chimpanzee breeding cycles indicate that poaching of only 25-100 reproductive females (in an effort to obtain their young for the live trade) could cause extinction of a population of 10,000 chimpanzees in less than 50-100 years. When poaching is conducted at random or mothers are spared, the population sex ratio always remained nearly 50:50. However, when mothers are killed, the sex ratio always becomes heavily skewed in favor of adult males. In many simulation series, the population is comprised of more than 70% adult males within only 50-80 years, with as many as 2,000 males remaining in the population for up to two decades prior to extinction. These results indicate that a seemingly "healthy" population of 1,000-2,000 chimpanzees may actually be poised on the brink of extinction if poachers focus their attention primarily on mother-infant pairs.

International Trade in Chimpanzees: Problems and Solutions

Michael A. O'Connell World Wildlife Fund, Washington, D.C.

Kurt A. Johnson TRAFFIC USA, Washington D.C.

The chimpanzee (*Pan troglodytes*) has disappeared from much of its historic range, and remaining populations are declining rapidly. Despite more than 15 years of international regulation, and legal protection in many countries, trade remains a primary factor in the species' decline.

The United States, Western Europe, and Japan imported the majority of chimpanzees in recent decades. Theoretically these countries provide stringent trade control. In particular, several U.S. laws prohibit commerce in the species. Yet the high black market price of chimpanzees can lead to abuse of trade regulations.

No previous study has thoroughly reviewed international chimpanzee trade or assessed existing regulations and their implementation. Accordingly, this paper begins with a background on CITES and other regulations. It then seeks to quantify statistics from importing nations and draw conclusions about the nature of trade. U.S. data, although of questionable completeness and accuracy, nevertheless provide the best insight. Through documentation of illegal trade cases, the study examines trade routes outside international law. Finally, based on problems revealed in the analysis, the study recommends potential solutions to abuse of CITES and to illegal chimpanzee trade.

Conservation Issues in Africa (Slide Presentation)
Chimpanzees: Do They Have a Future in Africa? (Slide Presentation, Public Session)

Michael "Nick" Nichols

Member, Magnum Photos, New York, and contributor to National Geographic, Washington, D.C.

A selection of photos shot for *National Geographic's* March 1991 feature, "Apes and Humans," was presented. The photos were the result of months spent in the forests and jungles of Africa, where intimate images of chimpanzees were captured in Tanzania, Ivory Coast, Sierra Leone, Liberia, Burundi, and Zambia. Contrasting with idyllic pictures of life in the wild are powerful and disturbing images of chimpanzees living in captivity: chained up as pets, physically altered for entertainment, and isolated in small, sterile cages in biomedical labs (where chimps used in AIDS and hepatitis research are often totally deprived of social contact). These photographs raise important ethical questions about the relationship between chimpanzees and humans, and they publicize the plight of chimpanzees in captivity around the world. A selection of this work will be featured in the book *Brutal Kinship*.

COUNTRY REPORTS

Uganda Update

Richard W. Wrangham

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts

Most of Uganda's roughly 4,500 chimpanzees live in nine discrete forest blocks under the control of the Forest Department or National Parks. The chimpanzee population appears stable. Uganda shows a positive attitude toward habitat and wildlife conservation: (1) The Forest Department has evicted encroachers from all Forest Reserves except Kibale. (2) Eco-tourism with special focus on chimpanzees is being developed in Kibale Forest and in Queen Elizabeth National Park. Forest tourism projects are also planned in the Impenetrable Forest and Budongo Forest. (3) Several Forest Reserves (where logging can be allowed) are being converted to National Parks, including the Ruwenzori Mountains and Impenetrable Forest. (4) The use of Uganda as a smuggling port has been reduced by confiscations of illegally held chimpanzees. Habitat conservation is seen both by Ugandans and by aid organizations as a key component of a stable future; chimpanzee conservation is viewed as important in that effort.

Status of Chimpanzees in Gabon

Caroline E. G. Tutin

Centre International de Recherches Médicales de Franceville, Gabon, and Scottish Primate Research Group, University of Stirling, Stirling, Scotland

Michel Fernandez

Centre International de Recherches Médicales de Franceville, Gabon, and Scottish Primate Research Group, University of Stirling, Stirling, Scotland

Gabon, situated on the equatorial coast of West Africa, harbors probably the largest surviving population of chimpanzees on the continent: The results of a nationwide census of chimpanzees in Gabon, completed in 1983, yielded encouraging results. The total population was estimated at 64,000, with an assessed accuracy of plus or minus 20%. Is this, as many people have implied, a lot of chimpanzees? In response, we note that (1) this total represents mean densities in areas of suitable habitat of under 0.3/km²; (2) we found areas where chimpanzees had been eradicated by hunting or habitat destruction; and (3) no chimpanzees live in National Parks, and although they are legally protected from hunting and capture, some hunting does occur.

While the long-term future of these chimpanzees is far from secure, the potential for "conservation before a crisis" still exists in Gabon. The historical factors that provided "natural" protection are changing and the well-known threats of habitat alteration and hunting are encroaching on the sanctuary that Gabon's intact tropical forest represents. The experience of other African countries emphasizes how precarious the present situation is and how rapidly dramatic declines in chimpanzee populations and fragmentation of remaining populations can occur. In this paper we will try to establish an optimal approach to conservation in Gabon, taking into account cultural and economic realities.

Census and Distribution of Chimpanzees in Côte d'Ivoire

Paul Marchesi

Institute of Zoology, University of Basel, Basel, Switzerland

Nathalie Marchesi

Institute of Zoology, University of Basel, Basel, Switzerland

Christophe Boesch

Institute of Zoology, University of Basel, Basel, Switzerland

Methods of estimating chimpanzee population densities rely mainly on nest counts. We tested the most frequently used techniques on a known chimpanzee community living in the rainforest of the Tai National Park, Côte d'Ivoire. The best density estimates are given by counts that consider groups of nests to be distributed randomly and that use the mean of group size for homogeneous habitat but the median for heterogeneous habitats. Correction for the real forest cover within a region should be

made because chimpanzees make nests only in forested regions. This method gave the exact chimpanzee density for the Tai population, e.g., 1.7 nest builders/km². For the nation-wide survey, we first estimated the chimpanzee density for different types of habitat (e.g., intact primary forest: 1.64 chimpanzees/km²; degraded forests: 0.4 chimpanzees/km²; human-encroached forests and mosaic habitats: 0.09 chimpanzees/km²). Second, we estimated the total forest cover of the country with satellite pictures. This gave us an estimated chimpanzee population in Côte d'Ivoire of about 11,676 +/- 1,168 individuals. Sadly, only three National Parks have chimpanzee populations large enough to be viable in the long term, whereas the rest are scattered and isolated small populations that are already threatened in their survival.

Bonobo Conservation in the Wild

Suehisa Kuroda

Department of Zoology, Kyoto University, Kyoto, Japan

The bonobo population is rapidly decreasing due to hunting and deforestation. The population is estimated to be less than 20,000 and the bonobo habitat has been reduced by almost half since 1975.

The Wamba Research Team established the Bonobo / Pygmy Chimpanzee Protection Fund and started the Luo Project in 1991, supported by the Bonobo Protection / Conservation Fund at Georgia State University. The aim of the project is to protect the 3,000 bonobos inhabiting the forest of the upper Luo River.

The Zoological Society of San Diego held a workshop in May 1991 for comprehensive bonobo protection/conservation. This workshop facilitated various projects for bonobo conservation. However, the politically chaotic situation in Zaire put a stop to all projects. We are waiting for improvement of the situation in this region.

An Experiment in Long-Term Conservation

Annette Lanjouw

Tongo Chimpanzee Conservation Project, Zaire

The Virunga National Park, located in Eastern Zaire, still contains important numbers of chimpanzees (Pan troglodytes schweinfurthii) in forests ranging from 750 meters in altitude to about 2,000 meters. This area of Zaire is heavily populated and the park is entirely surrounded by agricultural fields. The Tongo Chimpanzee Project has as its aim the protection of a population of wildliving chimpanzees and their habitat, as well as the logistical support of the institution charged with their protection. The method used to achieve these aims is the development of a controlled eco-tourism program whereby

visitors observe habituated chimpanzees in their natural habitat without undue disturbance. Trained guides provide information on the animals' behavior. The project was initiated in 1987 by the Frankfurt Zoological Society with funding from the Messerli Foundation, Switzerland. In 1990 tourism was initiated, providing a source of income for the Zaire Institute for the Conservation of Nature (IZCN) and an incentive for conservation. The chimpanzees are regularly monitored and the forest is patrolled for poaching activity.

Country Reports and Conservation Updates
See also Research Site Overviews (Kano, Isabirye-Basuta et al., Sabater Pi and Veá)

SANCTUARIES

Chimfunshi Wildlife Orphanage

Carole Noon

Chimfunshi Wildlife Orphanage, Chingola, Zambia

In spite of their status as an endangered species, chimpanzees continue to be hunted to supply the demand for chimpanzee infants. Several African countries have increased their efforts to stop the illegal trade in chimpanzees. These efforts include confiscating infants on route to the international market and those being kept as pets. A growing problem across Africa is what to do with these chimpanzees once they have been confiscated.

One of the few qualified sanctuaries accepting these orphans is Chimfunshi Wildlife Orphanage located in Northern Zambia. Chimfunshi is the result of the determination and imagination of Dave and Sheila Siddle. The first chimpanzee arrived at Chimfunshi in 1983. Today there are 37 chimpanzees living there. The chimpanzees live in two groups in large outdoor enclosures (one is 7 acres and the other 11 acres) on the Siddle's farm. The chimpanzees will ultimately be moved to a 2,000—acre section of the farm that the couple has designated as a permanent sanctuary.

RESEARCH AND CONSERVATION IN CAPTIVITY

RESEARCH

Environmental Enrichment in Captivity

Mollie Bloomsmith

Department of Veterinary Resources, University of Texas M.D. Anderson Cancer Center, Science Park, Bastrop, Texas

Captive chimpanzees living in zoological parks, breeding colonies, and biomedical research centers share a number of behavioral problems which must be addressed by those people caring for the chimpanzees. Enrichment strategies to overcome behavioral management problems need to encompass the social lives of the chimpanzees, as well as non-social aspects such as feeding strategies, the physical contents of enclosures, occupational tasks, and sensory stimulation. Behavioral research that quantitatively documents the effects of a variety of environmental enrichment techniques is reviewed. The goal of such investigation is to develop a scientific foundation for improving care and management of captive chimpanzees. The current state of this body of knowledge is critiqued, with suggestions concerning future directions. The need to gain cooperation from people working with chimpanzees at many different types of facilities is emphasized.

ChimpanZoo: Looking at Chimpanzee Behavior in Contemporary Zoos

Virginia Landau

Program Director, ChimpanZoo, The Jane Goodall Institute, Tucson, Arizona

James E. King

Department of Psychology, University of Arizona, Tucson, Arizona

Maryanne Clark

Department of Biology, Texas Wesleyan University, Fort Worth, Texas

Exhibits in contemporary zoos reflect a change of emphasis. In the past, zoos were characterized by utility of containment, care, and exhibition (e.g., sterile tile, glass cages, and deep smooth-walled structures). Modem zoo architecture utilizes multiple substrate levels and combinations of vegetation, objects, structures, and moveable objects to produce a naturalistic habitat for chimpanzees. The diversity and complexity of these chimpanzee habitats makes conducting behavioral research in multiple zoos an ambitious endeavor.

Using an ethogram developed, tested, and refined over a three-year period, ChimpanZoo is conducting research in multiple zoo sites. The ChimpanZoo system allows for the collection of two kinds of data – social context and specific behaviors – both of which show high reliability as measured by the Kappa statistic. In addition to behavioral data, the ChimpanZoo system will contain information on the life histories of the chimpanzees, the zoo characteristics, individual differences, and demographic variables related to a wide assortment of behaviors. All of this information has important implications for zoo habitat improvement and enrichment.

ChimpanZoo (Video Presentation)

Virginia Landau

Program Director, ChimpanZoo, Jane Goodall Institute, Tucson, Arizona

James E. King

Department of Psychology, University of Arizona, Tucson, Arizona

Maryanne Clark

Department of Biology, Texas Wesleyan University, Fort Worth, Texas

One of the exciting aspects of ChimpanZoo, a multiple zoo study, is the ability to make comparisons. With more than 100 chimpanzees in the study, we can easily observe diversity of behavior among and between chimpanzee populations. In addition, we are able to record the effects of environmental factors on individual and group behavior. The ability to investigate behavioral variation is greatly enhanced when used in conjunction with the ChimpanZoo database of individual chimpanzee life histories and personality assessments.

Using Novel Objects to Facilitate Exploration and Play, and Reduce Aberrant Behaviors in the Chimpanzee Group at Adelaide Zoo (Poster Presentation)

Carla Litchfield

Department of Psychology, University of Adelaide, Adelaide, South Australia

Six novel objects were introduced into the outdoor chimpanzee enclosure at Adelaide Zoo. These objects were designed to facilitate exploration and play in the group of six chimpanzees, thereby reducing aberrant behaviors (such as coprophagy and fecal art, or smearing). One set of objects could be manipulated to obtain food, while a second set was purely for exploration. The importance of taking the principles of exploratory behavior (e.g., novelty and complexity of stimulis, and habituation) into account when designing behavioral enrichment objects for chimpanzees is stressed. Behavioral similarities and differences were noted between this group of six chimpanzees and those housed at Melbourne Zoo, Taronga Zoo, and Perth Zoo.

CONSERVATION

An Overview of the Chimpanzee Species Survival Plan

Les Schobert

General Curator and Chimpanzee SSP Coordinator, North Carolina Zoological Park, Asheboro, North Carolina

In 1981 the American Association of Zoological Parks and Aquariums (AAZPA) recognized the need for zoos to play a prominent role in global conservation and established the Species Survival Plan (SSP). The goal of SSPs is to scientifically manage and sustain long-lasting captive populations. Besides sound genetic management, behavioral and social factors must also be addressed. A holistic approach becomes increasingly important as we learn more about the social structures and reproductive biology of the species.

The chimpanzee SSP's goal is to retain 90% of the founders' genetic diversity for 200 years. *A carrying capacity of 200 to 250 animals is needed to maintain a self-sustaining population. The current captive population of 214 chimpanzees in the U.S. nearly fills the existing spaces for adult animals; additional space will be needed, since 63% of the individuals are 10 years old or less. No additional animals need to be imported into the population. The growth rate of the chimpanzee SSP population is being kept intentionally low due to the lack of space.

The SSP is concentrating on the one aspect of chimpanzee conservation that is under our auspices – the care of captive chimpanzees – but we remain committed to chimpanzees as a species.

The Bonobo Species Survival Plan: Beyond Captive Management

Gay E. Reinartz

Species Coordinator, Bonobo SSP, Zoological Society of Milwaukee County, Milwaukee, Wisconsin

The Species Survival Plan (SSP) is a voluntary propagation program designed to create and maintain self-sustaining captive populations of endangered wildlife. The Bonobo SSP coordinates the captive breeding and management of bonobos held by zoological institutions throughout North America.

Fewer than 90 bonobos comprise the world captive population; intensive genetic and demographic management is necessary to overcome risks associated with small population size. Behavioral considerations, as well as demographic/genetic data, provide the basis for formulating management objectives and breeding recommendations. The Bonobo SSP's mission is to optimize the utilization of the captive population as a conservation resource, especially in areas such as conservation research and education. The mission includes working in concert with other conservation organizations to develop complementary programs for bonobo conservation in Zaire. The role the Bonobo SSP will play in global conservation is evolving, but zoos are working to extend their efforts beyond traditional zoo management.

Bonobo Conservation Task Force Update

Bill Konstant

Flagship Species Program, Conservation International / Philadelphia Zoo, Philadelphia, Pennsylvania

In May 1991, the Zoological Society of San Diego hosted the Bonobo Conservation Workshop, attended by more than 50 specialists on the bonobo or pygmy chimpanzee (*Pan paniscus*). As a result of this workshop, a Bonobo Conservation Task Force was established, co-chaired by Dr. Russell Mittermeier, President of Conservation International and Chairman of the IUCN/SSC Primate Specialist Group.

Since the workshop, the Bonobo Conservation Task Force has submitted a five-year proposal to the World Bank to support conservation of bonobo populations and tropical rainforest habitat in Zaire's Equateur Province. This proposal addresses all the major concerns for the survival of *P. paniscus* expressed in San Diego and includes provisions for region-wide censuses and surveys, longterm research projects, development of protected areas, professional training of Zairian biologists and fieldworkers, national institutional development, conservation education and public awareness programs, eco-tourism, and captive breeding programs.

As we wait to see what will result from the current political, social, and economic turmoil in Zaire, the Bonobo Conservation Task Force is preparing an Action Plan and identifying the manpower and financial resources necessary for its implementation.

Captive Care and Management in Japan

Tetsuro Matsuzawa

Department of Psychology, Primate Research Institute, Kyoto University, Aichi, Japan

This talk examined the present situation of chimpanzees in Japan. Approximately 50 zoos, two universities, and one medical company possess about 320 chimpanzees in total. There is no research in Japan for hepatitis or AIDS using these chimpanzee subjects. Although their lives are not threatened, the chimpanzees are kept in facilities which afford far from ideal conditions.

RELATED CONTRIBUTIONS (POSTERS AND WORKSHOPS)

RESEARCH SITE OVERVIEWS

Mahale Update (Poster Presentation)

Toshisada Nishida Department of Zoology, Kyoto University, Kyoto, Japan

The Mahale Mountains Chimpanzee Research Project, in Mahale Mountains National Park, Tanzania, is organized by Toshisada Nishida, Kyoto University. The principal investigators are Kenji Kawanaka, Okayama University of Science, and Shigeo Uehara, Sapporo University. Recent areas of research include pant hoots (John Mitani, 1989-1990), behavior of young adult males (Kenji Kawanaka, 1990), sibling relationships (Miya Hamai, 1991), DNA paternity testing (Hiroyuki Takasaki, 1991), male politics (Toshida Nishida, 1991), intestinal parasites (Kozo Yoshida, 1991), vocal communication (Kazuhiko Hosaka, 1991-1992), mother-infant communication (Hiroko Yoshida, 1991-1992), juvenile behaviors (Akiko Matsumoto, 1991-1992), medicinal plants (Michael Huffman, 1991-1992), taphonomy (Nicholas Kiltzer, 1991-1992), and distribution (Edeus Massawe, 1992). Recent publications include *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, edited by T. Nishida, 1990, University of Tokyo Press, Tokyo.

Wamba Update (Poster Presentation)

Takayoshi Kano

Primate Research Institute, Kyoto University, Aichi, Japan

At least six unit groups of bonobos have all or part of their home ranges within the Wamba forest (ca. 150 km²). The bonobo population is estimated at ca. 300. Study efforts are focused on three of the unit groups (El, E2 and P), under provisioned and habituated conditions. The sizes of the El, E2 and P groups are ca. 30, 55 and 45, respectively. Although the human inhabitants (ca. 1,000) do not hunt bonobos for food, subsistence activities such as clearing the forest, as well as poaching by outsiders, have become a serious menace to the survival of bonobos at Wamba. In early 1990, the government of Zaire established the "Scientific Reserve of Luo" for the purpose of protecting bonobos. The reserve consists of the Wamba and southern Ilongo forests, covering an area of ca. 350 km². This action provided the legal basis for bonobo protection in the region.

Kibale Update (Poster Presentation)

G. Isabirye-Basuta

Department of Zoology, Makerere University, Kampala, Uganda

Colin Chapman

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts

Kevin D. Hunt

Department of Anthropology, Indiana University, Bloomington, Indiana

Richard W. Wrangham

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts

The Kanyawara community has been monitored continuously since 1987, following an 18-month gap in observation during which almost half the known individuals disappeared. There are currently about 40 individuals. The composition of the Ngogo community is still unknown, but there appear to be a large number of adult males (perhaps 20). The initiation of a tourism project at Kanyanou ("Dura River") in mid-1991 means that a third community of chimpanzees will now come under observation. Snares set for antelope are an important threat to chimpanzees in Kibale: two individuals in Kanyawara showed fresh snare wounds (January 1990, November 1991). Research opportunities are becoming easier with the development of the Makerere University Biological Field Station into a research institute of international caliber. Continuing research projects include the relation between diet and food availability, social dynamics, and feeding competition.

Pan paniscus in the Lokofe-Lilungu Region, Zaire (Poster Presentation)

Jordi Sabater Pi

Department de Psiquiatria i Psicobiología, Facultat de Psicología, Universitat de Barcelona

Joaquim J. Veá

Department de Psiquiatria i Psicobiología, Facultat de Psicología, Universitat de Barcelona

Over a period of two years (1988-1990), we studied the distribution, ecology, and behavior of the bonobo chimpanzee (*Pan paniscus*) in the Lilungu region (1° 7' 36" S and 23° 1' 28" E) of central Zaire. The study area covers approximately 72 km², from the Ikela-Lokofe-Ikomaloki trail to the Tshuapa River between Lokofe and Ikomaloki. As a result of human activity in the area, the vegetation appears in a mosaic pattern due to the various levels of regeneration.

The population density of *Pan paniscus* was estimated using a nest census and the techniques of Anderson et al., Burnham et al., Laake et al., Ghiglieri, Tutin and Fernandez, and Crain et al. Compensation was made for day nests and for lack of nest construction by non-adult individuals. A possible source of error is the fact, repeatedly observed by Kuroda, that bonobos are known to share

nests. We obtained a density estimate for bonobo chimpanzees 0.4/km². We found that 28% of the nests were in the fully-developed secondary forest covering 65% of the study area. The remaining nests (72%) were found in 17% of the area, which included agrological forest, areas of Beluccia, and young secondary forest; the young secondary forest contained 41 % of the nests.

Chimpanzees Pan troglodytes troglodytes) of the Ndoki-Nouabale Forest, Northern Congo (Poster Presentation)

Suehisa Kuroda

Department of Zoology, Kyoto University, Kyoto, Japan

Rufin A. Oko

Ministry of Forestry Economy of the Congo

Eleven higher primates, including chimpanzees and gorillas, inhabit the Ndoki-Nouabale Forest. Chimpanzee unit groups appear to have 30-40 members. They have the same grouping pattern and greeting behavior as the East African chimpanzees. Promiscuous mating involving the alpha-male was observed. The birth intervals of several females were estimated at 3-4 years, the shortest in any chimpanzee population ever studied.

The chimpanzees are basically frugivorous, but leaves and buds of *Celtis* sp. become the main food in the rainy season. The chimpanzees eat ants and termites, using two types of tools: digging sticks and long brushes. Predation by chimpanzees seems rare.

Both the chimpanzees and the gorillas depend on the same kinds of fruits in the fruiting season, often using the same area. (In January, cases of co-feeding by these two species were observed by Mr. Suzuki.) Gorillas become purely herbivorous when fruits are scarce, so severe interspecies competition does not occur.

Nest Building in Wild Bonobos Pan paniscus) in the Lomako Forest (Poster Presentation)

Barbara Fruth

Department of Zoology, University of Munich, and Max Planck Institute for Human Ethology, Andechs, Germany

Gottfried Hohmann

Department of Zoology, University of Munich, and Max Plank Institute for Human Ethology, Andechs, Germany

Although chimpanzees spend more than half of their lives in nests, knowledge of nest building behavior is still fragmentary. During a one-year field study in the Lomako Forest of Zaire, data on the ecology and ethology of bonobo nest-building were collected. A total of 771 nests was analyzed in detail. Most of the nests (79%) were located between 10 and 30 meters above the ground; 35% of

the nests were integrated nests (involving two or more trees). Conspicuous differences in the morphology of the nests and behavior of the builders became apparent when the time of nest construction was considered. Height of nests and duration of construction revealed sex-specific differences. Comparison of the metrical and morphological data obtained in this study, with previous reports from other areas, suggests population-specific differences.

Day nests were not only used for rest, but also for feeding, social grooming, and play. Moreover, recordings of behavioral interactions over food and agonistic interactions revealed that day nests may also be "taboo zones," restricting or preventing invasion of other unit-group members.

Ishasha River Project (Poster Presentation)

Jeanne Sept

Department of Anthropology, Indiana University, Bloomington, Indiana

Horst D. Steklis

Department of Anthropology, Rutgers University, New Brunswick, New Jersey

Mubalama Kakira

Conservateur Scientifique, Chef de Station Scientifique de Lulimbi, Parc National des Virunga, Institute Zairois pour la Conservation de la Nature, Zaire

A collaborative ecological study of free-ranging, unhabituated chimpanzees (*P. t. schweinfurthii*) living along the Ishasha River in the Virunga National Park, eastern Zaire, was begun in June-August 1989 and continued in April-August 1990. Nest surveys resulted in density estimates of between 3 and 7 nest-building chimpanzees per square kilometer of forest. The average total population was estimated at 24 nest-building chimpanzees in the Ishasha River region. To investigate the resource availability in this semi-arid gallery forest habitat, the fruiting productivity of known chimpanzee food trees was estimated, phenological plots were monitored to follow the seasonal availability of different food types in different microhabitats, and fresh chimpanzee fecal samples were collected and analyzed for dietary evidence. The distribution and frequent reuse of nesting and feeding sites in the forest was mapped along transects to compare the ranging behavior of the Ishasha chimpanzees with the patterns of early hominid land-use reconstructed from archaeological evidence in similar East African habitats.

GENETICS

Non-Invasive Sampling of DNA from Wild Chimpanzees (Workshop Presentation)

Hiroyuki Takasaki

Center for African Area Studies, Kyoto University, Kyoto, Japan

Osamu Takenaka

Primate Research Institute, Kyoto University, Aichi, Japan

Conventional samples used for biochemical analysis (e.g., blood) are difficult to collect from chimpanzees in the wild. Even if successfully collected, such samples need special care in preservation and transportation (e.g., freezing). Such requirements cannot be met at most field sites in the chimpanzees' natural habitats, which are located in remote areas of Africa.

A set of technological innovations — in vitro amplification of DNA using the polymerase chain reaction (PCR) method with thermostable DNA polymerases — has recently added minute body fragments, such as single hairs, buccal cells in wadges, etc., to the list of samples that can be used for DNA analysis. Such minute body fragments can be collected by non-invasive techniques and are easily preserved. Thus, DNA amplified from hairs and buccal cells has a wide spectrum of potential applications in genetic studies in the field (e.g., paternity testing). The present study investigates the suitability of this method for paternity testing in chimpanzees. Shed hairs collected from self-grooming individuals or from beds may be simply wrapped and kept dry in paper (such as entomological envelopes). Wadges of fibrous plant food may be preserved in > 50% ethanol (final concentration) for later DNA extraction, amplification, and analysis in the laboratory.

Application of New Genetic Techniques (Workshop Summary)

Maryellen Ruvolo

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts

Hirovuki Takasaki

Center of African Area Studies, Kyoto University, Kyoto, Japan

The advent of polymerase chain reaction (PCR) technology means that sampling field or zoo animals for genetic determinations can be physically non-invasive and behaviorally non-disruptive. One or two shed hairs, stored in ethanol or kept dry, can provide enough material for DNA sequence determination. In addition, chimpanzee wadges, preserved in ethanol at room temperature, contain enough cells for DNA studies. Active areas of research using these genetic methods include (1) paternity determination using DNA fingerprinting (e.g., by David Woodruff, John Ely, and Hiroyuki Takasaki) and (2) assessing chimpanzee and bonobo variation within and between species (e.g., by Woodruff, Ruvolo, Takasaki). Ruvolo and Takasaki propose an informal newsletter to coordinate efforts, share methods, and avoid duplication of work for those interested in genetic studies.

Strategies for the Genetic Management of Captive Chimpanzee Colonies (Poster Presentation)

S. Williams-Blangero

Department of Genetics, Southwest Foundation for Biomedical Research, San Antonio, Texas

B. Dyke

Department of Genetics, Southwest Foundation for Biomedical Research, San Antonio, Texas

Maintaining population variability and avoiding inbreeding is vital for captive chimpanzee colonies because they are closed to the introduction of wild-caught animals. Simple methods, using readily available data, can be used to achieve these genetic management goals. The basic pedigree can be obtained from records of sire and dam for each individual. These records are then linked, using computer software such as PEDSYS (a pedigree based data management system), to reconstruct extended pedigrees. Only when multi-male breeding schemes are used are biomedical and DNA markers needed for establishing the basic pedigree. Pedigree data provide the basis for simulation analyses to determine a colony's effective size and expected levels of heterozygosity. Routinely characterized quantitative traits (such as clinical chemistries) provide a rich source of information for monitoring variability. Thus, organizing available animal records into a form suitable for genetic analysis allows rapid initiation of genetic management programs at minimal cost.

INTERACTIVE MEDIA

The Jane Goodall Research Center at the University of Southern California: Using an Interactive Multimedia System (Demonstration)

Gary Seaman

Director, Jane Goodall Research Center, University of Southern California, Los Angeles, California

Homer Williams

Center for Visual Anthropology, University of Southern California, Los Angeles, California

The Jane Goodall Research Center is developing a data research system based on the easy access to data provided by HyperCard text and graphics software (loaded on all Macintosh computers). In conjunction with a VHS tapedeck or videodisc player, the system allows a researcher to navigate through various databases, select and organize topical information, and target visual representations related to the selected topics. Contextualizing information can then be organized within the system for publication in conjunction with (or integrated into) audiovisual productions. Some functions supported by the system include referencing, source locations, geographical information and mapping, topic and keyword searches, and database prototyping. In addition, the system serves as an inexpensive means of logging audiovisual materials for any computerized program.

OTHER RECENT ACADEMY PUBLICATIONS

Science Learning in the Informal Setting Published

by The Chicago Academy of Sciences

Paul G. Heltne and Linda A. Marquardt, Editors

What key scientific concepts help citizens understand events and empower them to participate effectively in important decisions? How can museums, schools, parks, zoos, and other informal science centers make the greatest impact on the children of today? Prominent scientists, educators, and museum planners gathered at The Chicago Academy of Sciences in November 1987 to discuss the role that informal science learning centers play in advancing science literacy. Papers presented at this highly charged four-day symposium have been published in a 350-page volume. Available through The Chicago Academy of Sciences. \$18.95, paperback.

Understanding Chimpanzees

Published by Harvard University Press in cooperation with The Chicago Academy of Sciences

Paul G. Heltne and Linda A. Marquardt, Editors Foreword by Jane Goodall

Chimpanzee specialists from around the world contribute to this landmark volume resulting from the first international conference on chimpanzees, held in Chicago in 1986. *Understanding Chimpanzees* examines social behavior and ecology in the field, behavior in captivity, and the cognitive abilities of chimpanzees in language acquisition laboratories. The book contains a major section on chimpanzee conservation in captivity and in the wild, strong coverage of bonobos (pygmy chimpanzees), and important contributions by Japanese researchers, whose work is not readily accessible in the West. In addition to the Foreword, Jane Goodall contributes a review of her work at Gombe, her progress with "ChimpanZoo," and an update on the status of conservation in Tanzania. Over 100 photographs and drawings illustrate the text. *Available through The Chicago Academy of Sciences, Harvard University Press, or bookstores. \$40.00, hardcover.*

